

The following papers were read :—

1. On the Scales of Fish, Living and Extinct, and their importance in Classification. By EDWIN S. GOODRICH, F.R.S., F.Z.S., Fellow of Merton College, Oxford.

[Received November 12, 1907.]

(Plates XLIII.—XLVI.\* and Text-figures 196–204.)

In a recently published paper on the Dermal Fin-rays of Fish (3), I remarked that the importance of the scales in classification seemed not to have received the attention it deserved. A careful study of the structure of the scales of living and extinct fish having confirmed this opinion, an account is here given of the results of my researches. Incomplete as these are, partly owing to the lack of material, they will be sufficient, I think, to show that the subject is full of interest, and well worthy of further study.

For the material used in the investigations I am to a great extent indebted to the generosity of various friends, among whom may be mentioned Dr. Traquair, Prof. Sollas, and Mr. Boulenger; but especially do I wish to express my thanks to Dr. A. Smith Woodward for help constantly rendered during my frequent visits to the British Museum.

Agassiz, in his classical memoirs on fossil fish (1), laid the foundation of the modern work on fish-scales, and it is well-known that he based his classification chiefly on their structure. But less generally known is it that more than half a century ago Williamson (26 & 27) published two most important papers on the scales of fish, of which he gave a very detailed and beautiful account. Not only was he able in many ways to complete and correct previous observations, to give the first accurate description of the minute structure of the scales of living and extinct Selachii, 'Ganoidii,' and Teleostei, but he also explained their mode of growth, and brought forward a theory of the origin of the various types of scales, and of their derivation from the primitive denticles of the Elasmobranch. Indeed Williamson's theory is in many respects superior to those modifications of it which have since been published by Hertwig (7), Klaatsch (10), and others. It may be added that in these remarkable papers Williamson clearly distinguished calcification of cartilage in the Elasmobranch from the various processes of the formation of true bone he described in other fish. His theories will be discussed later on (pp. 759–760); but it may here be mentioned that he considered that the superficial layer of the scale of *Megalichthys* is formed by the combination of a layer of "cosmine," derived from denticles homologous with those of Elasmobranchs, with deeper layers of bone of independent origin. He believed the cosmine layer to be formed by the concrescence of "dermal teeth." He further showed that the outer

\* For explanation of the Plates, see p. 774.

layers of a ganoid scale are not formed of true enamel, but are continuations of the lower layers which overlap on to the upper surface, the scale growing by the deposition of complete concentric lamellæ. The Teleostean scale he described as growing in the same way, and as derived from the Ganoid.

At the time Williamson made these interesting observations, the classification of fossil fish was in a very unsatisfactory state. Allied forms were frequently widely separated, or distantly related forms closely grouped together. It is not surprising, then, that the systematic importance of his work should have escaped the notice of ichthyologists as well as of the author himself. Now that the classification is so much better understood, we cannot help being struck by the value of the evidence afforded by his researches; and it is mainly for the purpose of calling attention to them that this paper has been written.

#### TYPES OF SCALE.

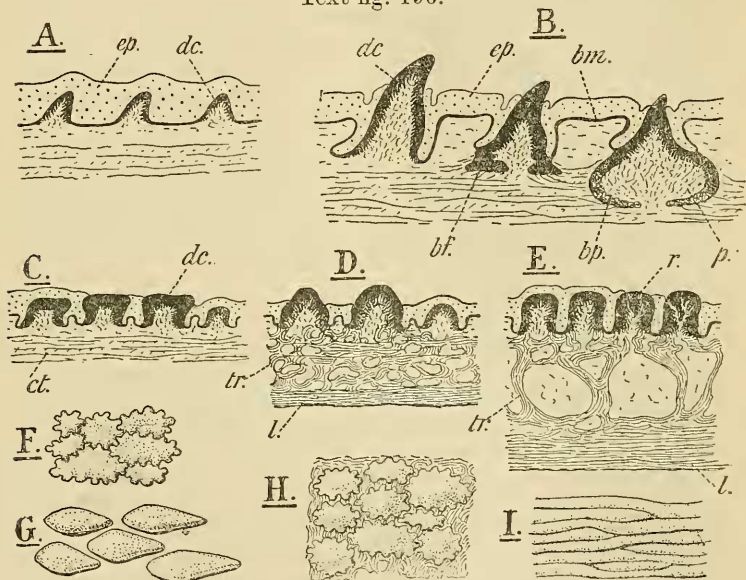
**The Placoid Scale.**—Little need be said concerning the denticles of Elasmobranch fish; attention must, however, be drawn to a few important points. True denticles are universally present in the living Elasmobranchs and their extinct allies. In structure they are remarkably constant, always consisting of a cap of dentine enclosing a pulp-cavity from which radiate numerous canaliculi (text-fig. 196). The cavity often becomes subdivided into branching canals uniting at the base, and giving off the dentinal tubules. The base is pierced by one or more openings through which the pulp can communicate with the surrounding mesoblastic tissues of the dermis. The dentine cap is covered on its outer surface with a layer of hard transparent enamel-like substance, the exact nature of which has given rise to considerable controversy. It is either true enamel deposited by the epidermis, or merely an outer specialised layer of dentine (Röse, 21), or a combination of both (Tomes, 22). For our present purpose we may call it enamel, allowing that Tomes' view is probably correct.

The important thing to notice is that from its earliest appearance in development onwards the dentine cap is in direct continuity with the basement membrane lying below the epidermis. Unlike bone, the dentine grows on one surface only, and that is the surface limiting the pulp-cavity. The placoid scale, then, always remains next to the epidermis, and never as a whole sinks down into the dermis (text-fig. 196). As it grows older it may, and generally does, acquire a well-marked basal plate of fixation (text-fig. 196, B). This plate is merely an extension inwards of the original cone, and it soon comes into connection with the deep fibrous layer of the cutis. As described by Hertwig (6), the connective-tissue fibres penetrate into the plate. Like the rest of the denticle, the basal plate is never composed of true bone, never contains bone-cells: it may be formed either of dentine, or of some less dense substance especially in its deeper parts. When the base is very large, as in the spines of Skates, the dentine may gradually change to a softer tissue composed of numerous trabeculæ

surrounding irregular spaces. Since scleroblastic cells are free to pass on both sides of the ingrowing base, it can increase in size in all directions.

One may summarise the chief points thus:—The placoid scale, or denticle, begins as a cone of dentine deposited by mesoblastic scleroblastic cells below the epidermis, in continuity with the basement membrane; a basal plate may be present in the form of a direct extension inwards of the cone, never as a separate element which becomes fused on to it secondarily; both the cone and the plate are composed of dentine or some allied substance, never of true bone; the cone may pierce the epidermis, when fully grown.

Text-fig. 196.



(From Lankester's 'Treatise on Zoology,' by permission of Messrs. A. & C. Black.)

Diagrams of the structure and development of the dermal skeleton of A, an early stage, and B, later stages of Elasmobranchs; C, *Thelodus*; D, *Psammosteus*; E, *Pteraspis*, all in section at right angles to the surface; the dentine is black. F-I. Enlarged views of the outer surface of the dermal skeleton of F, *Thelodus* head, G, *Thelodus* tail, H, *Psammosteus* shield, and I, *Pteraspis* shield. *bf.*, expanded basal plate; *bm.*, basement membrane; *ct.*, connective tissue; *dc.*, dentine cap; *ep.*, epidermis; *l.*, bony lamellæ; *p.*, pulp-cavity; *r.*, surface ridge; *tr.*, bony trabeculae of vascular layer.

Such denticles are found in the Selachii and Holocephali, which are devoid of other forms of scaling. Probably they also occur in the Pleuropterygii (Cladoselachii) and Ichthyotomi (Pleuracanthodii); though details concerning the histological structure of the scales of these fish are still lacking. Rarely the denticles seem to fuse together, as for instance in *Hybodus* (28). The circumorbital

plates of *Cladoselache*, and the dermal plates of certain Holocephali (29) may also be of this nature, since they appear to be formed of dentine-like substance.

*The Scales and Plates of the Heterostraci.*—The important researches of Traquair (23 & 24) have disclosed a most interesting series of Palæozoic fish in which it appears to be possible to trace clearly the evolution of the bony carapace of the Pteraspids from the simple placoid scales of *Thelodus*. The latter (text-fig. 196, c & f) are broad and flattened denticles closely set in a mosaic on the head and trunk, and fitting together by their crenulated edges. In the tail region they lose the crenulations, are set farther apart, and are more spine-like in shape (text-fig. 196, g). Rohon (18) and Rôse (21) have described their finer structure. The pulp-cavity is simple, and there is no distinctly marked basal plate. The whole scale is formed of typical dentine. *Psammosteus* is almost entirely covered with large plates (Traquair, 23). Superficially these are studded with small denticles in every way similar to those of *Thelodus* (text-fig. 196, h). They have a rounded or pointed top, a wider base, and more or less closely-fitting crenulated edges. Below these denticles is a thick plate of bone-like tissue, which, however, is devoid of bone-cells. Since the structure of these plates has not been described in detail I give some figures of sections (Pl. XLIII. fig. 4, & text-fig. 196, d). An outer spongy layer, pierced in all directions by a network of vascular canals, occupies the greater thickness of the plate. It is indistinctly subdivided into two by a layer of lamellæ parallel with the surface. The inner side of the plate is strengthened with a thick lamellated layer. These skeletal structures have been deposited in successive laminae, as is evidenced by the striation seen in sections (Pl. XLIII. fig. 4). The plate grows in thickness by the addition of new layers on its lower surface.

The denticles are of quite different structure, are composed of true dentine very like that of *Thelodus* (Pl. XLIII. fig. 4), and contain a pulp-cavity. They rest on the underlying plate, to which they become fixed, being fused to it here and there at their base. But they are sufficiently separate to be frequently broken off in specimens. These denticles grow, of course, by the addition of new matter below; and so the pulp-cavity becomes very shallow, and is not exposed even when the cone is much worn down.

It is but a step from *Psammosteus* to *Pteraspis*, whose exoskeleton has been well described by Huxley (9) and Lankester (11). Here the denticles already elongated in some regions of *Thelodus* have been converted into long narrow, closely fitting ridges (text-fig. 196, i). Pander figures a fragment of a plate, probably of *Psammosteus*, which shows most beautifully intermediate stages in the elongation of the denticles (14). Each ridge of the *Pteraspis* shield shows in transverse section the structure of a typical placoid scale, with numerous tubules radiating from the elongated pulp-cavity into the dentine. Very narrow deep valleys

separate the dentine ridges, which may sometimes meet below. Traces of the crenulations may still be seen.

The underlying plate consists of an outer layer with very large vascular spaces, and a lamellated inner layer. The skeletal substance of which these are composed is quite similar to that of the *Psammosteus* plate.

Thus it appears that the shields of the Heterostraci, and also the scales and dermal fin-rays, have all been evolved by the combination of a covering of separate isolated denticles and an underlying plate, and the theory of Williamson is confirmed in a most remarkable manner by Traquair. But, and this is an important point, the superficial tubercles and the plate should not be compared to the pointed tip and expanded basal plate of an ordinary Selachian placoid scale. Throughout these changes the denticles remain essentially unaltered; the inner and continuous plate is evidently a quite distinct structure of separate origin—a new skeletal support doubtless developed in the cutis, and with which the denticles only came into secondary connection. In the most specialised forms (*Pteraspis*) the latter almost entirely lose their individuality, and acquire the deceptive appearance of being merely the ornamental surface of a scale or plate; yet they neither lose their characteristic tooth-like histological structure, nor do they really take part in the formation of the underlying plate.

*The true Scales.*—Coming now to the fish with true scales, we first of all study those scales which have hitherto been grouped under the name “ganoid.” Of these there are three types which can be clearly distinguished.

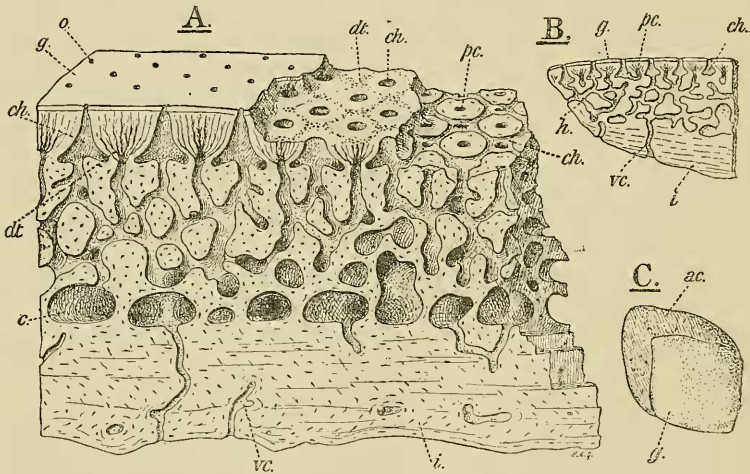
*The Cosmoid Scale.*—As an example of the first type, which may be called the “cosmoid” scale, we may take that of *Megalichthys*. It has been so well described by Williamson (23), that little need be said concerning its structure, which is shown in text-figs. 197 & 200. As usual, a basal layer is present composed of parallel bony laminae of “isopedine,” over which is a zone with large vascular spaces. Near the surface these canals combine to a more regular horizontal system forming a network passing round vertical canals, which reach the outer surface of the scale. It is the openings of these canals which give the pitted appearance to the shiny scales of the “Crossopterygian” fish. Below the surface the canals expand into conical chambers, between which pass upwards another set of vertical canals ending above in pulp-cavities. From these radiate a multitude of canaliculi.

A section parallel to the surface and just below it shows the conical chambers surrounded by a hexagonal pattern, formed by the cut ends of the dentine tubules (text-fig. 197). A section further down displays the pulp-cavities surrounded by the canals joining the chambers. This layer of vascular chambers and pulp-cavities disposed with such beautiful regularity may be considered as the highest development of “cosmine.” Williamson gave this name

to the peculiar dentine-like substance he discovered in "ganoid" scales. Unfortunately he also applied it to a very different bony tissue found in *Lepidotus* (p. 758). But in this paper the name cosmine will be restricted to a tissue with canaliculi like those of dentine, and the name "cosmoid" will be applied only to scales with an outer layer like that of *Megalichthys*.

The cosmine is restricted to that part of the outer surface of the scale which is exposed. Those regions which are overlapped by their neighbours in front have no cosmine, and are formed entirely of the two lower bony layers, the vascular and the isopedine (text-fig. 197, c). In both these are distributed numerous bone-cells. No such cells are found in the cosmine layer. The passage from the one to the other is gradual. Overlying the whole cosmine-covered surface is a thin layer of transparent glassy appearance and of homogeneous texture (text-fig. 197, A, & Pl. XLIII. fig. 5).

Text-fig. 197.



(From Lankester's 'Treatise on Zoology,' by permission of Messrs. A. & C. Black.)

Scale of *Megalichthys hibberti* Ag.; Carboniferous, England. A. Piece of a thick transverse section, much enlarged. B. Section through the hind edge, enlarged. C. Outer view of a scale. *ac.*, anterior region covered by next scale; *c.*, large vascular cavity; *ch.*, chamber of cosmine layer; *dt.*, canaliculi of cosmine; *g.*, thin outermost shiny layer; *h.*, irregular vascular canals; *i.*, bony inner layer or isopedine; *o.*, opening of chamber on surface; *pc.*, pulp-cavity from which canaliculi radiate; *vc.*, vertical canal.

Now, such a cosmoid scale grows at its edge and lower surface. New cavities may be excavated in the vascular layer, or old ones filled up; but the increase in bulk of the scale as it grows older can only take place by the addition of new lamellæ of isopedine below, and by the deposition of substance, enclosing new chambers

and pulp-cavities at the periphery (text-fig. 197, B). The cosmine layer with its thin enamel-like covering, is formed once and for all when it is first laid down. As far as one can judge from the examination of sections it does not materially alter with age. No new layers are deposited above it; such changes as take place are unimportant, and chiefly due to the filling up of the various spaces. The stratification of the isopedine indicates the lines of growth. Faint signs of laminae are also visible in the walls of the vascular spaces.

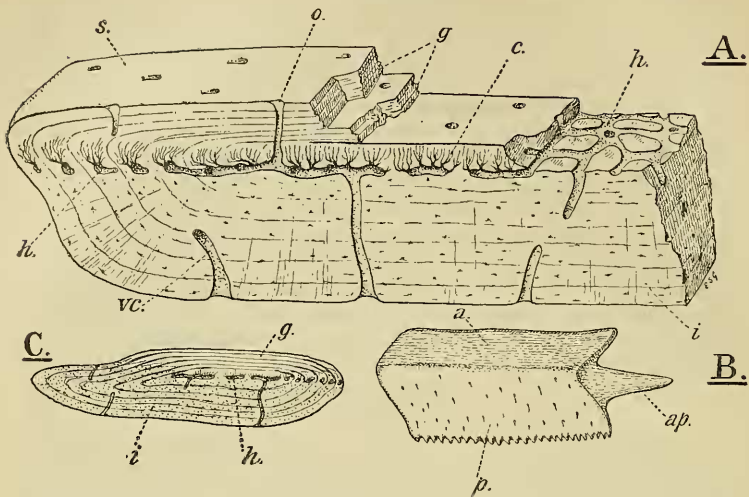
We may summarise the characters of the cosmoid scale as follows:—It has an outer layer of dentine-like substance with pulp-cavities and vascular chambers arranged in regular manner; a middle bony layer with vascular spaces; and an inner layer of bony laminae, probably ossified fibrous tissue of the cutis. The cosmoid scale grows in thickness only by the addition of new lamellae below; its outer surface is covered with a thin shiny layer, the nature and origin of which is uncertain.

**The Ganoid Scale.**—It is proposed to restrict the name “ganoid” to a type of scale found in all the Actinopterygii except the modern Teleostei. In its full development this type is represented by the rhombic scales of *Palæoniscus* and *Lepidosteus*. It differs radically from the cosmoid scale described above in that it grows in thickness by the addition of new layers not only below, but also on its upper surface. In fact concentric layers of new substance are continually being deposited over the whole surface; the oldest part of the scale is therefore at the centre. These layers, however, are not the same throughout; the lower being bony or fibrous, the upper of much denser homogeneous, enamel-like substance called ganoine by Williamson (text-fig. 198, c).

There are two distinct varieties of “ganoid” scale, differing in constant and important characters:—

*The Palæoniscoid Scale.*—*Gonatodus* or *Eurynotus* yields good examples of this type. The exposed surface of the scale is covered with a shiny layer of ganoine, pierced here and there by small vascular canals leading downwards into a horizontal network of canals (Pl. XLV. fig. 15, & text-fig. 198). From this again a few vertical canals pass downwards to open on the lower surface. The bulk of the scale, below the network of vascular spaces, is made up of the usual horizontal laminae of bone, arranged in parallel layers. At the periphery these layers are bent upwards and, so to speak, turned over to form the laminae of ganoine covering the outside of the scale. The two are continuous; but at their junction, just above the vascular spaces, is a cosmine-like layer penetrated by bunches of minute branching canaliculi passing upwards (fig. 15). Bone-cells are abundant below the vascular network, but none are found above it. Thus, in the Palæoniscoid scale, a layer of cosmine is interposed between the lower bony and the upper ganoine layers.

Text-fig. 198.



(From Lankester's 'Treatise on Zoology,' by permission of Messrs. A. & C. Black.)

*Eurynotus crenatus* Ag.; Lower Carboniferous. A. Diagrammatic and much enlarged view of a piece of the scale. B. Enlarged outer view of a scale. C. Transverse section of a scale, enlarged. *a.*, anterior covered region; *ap.*, articulating process; *c.*, fine canaliculi of cosmine layer; *g.*, ganoine layer; *h.*, system of horizontal canals; *i.*, isopedine layer; *o.*, opening on outer surface of vertical canals; *p.*, posterior exposed shiny surface; *s.*, outer surface; *vc.*, vertical canal.

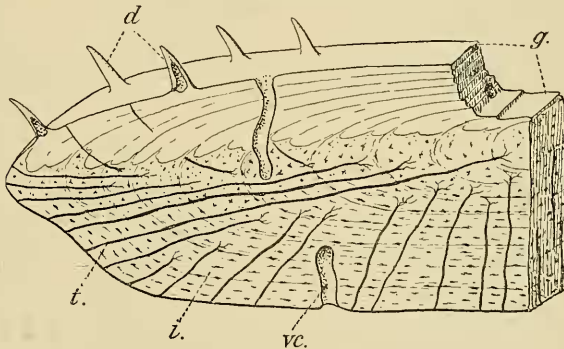
During growth the three kinds of tissue are laid down simultaneously and in continuity; but the articulating peg and the flange which is overlapped by the neighbouring scales are formed of bone only.

*The Lepidosteoid Scale.*—While resembling the Palæoniscoid scale in its general appearance and mode of growth, the scale of *Lepidosteus* differs from it in two important particulars (text-figs. 199 & 200). In the first place there is no horizontal network of vascular canals giving off canaliculi—there is therefore no regular zone of cosmine. In the second place, the scale is pierced by a multitude of slender unbranched tubules passing inwards from the surface at right angles to the lines of growth (Pl. XLVI. fig. 20). These tubules converge therefore towards the central or oldest region of the scale, and many of them penetrate to quite near the ganoine. As has been well shown by Hertwig (7) and Nickerson (13), each tubule belongs to one cell, which lies on the surface of the scale and sends a long process down the tubule. At their inner extremities the tubules break up into minute branching twigs. In some cases, as for instance in *Lepidotus*, these fine branches pass upwards at the edges with some regularity, where the bony lamellæ merge into the ganoine. Williamson speaks of this region



as cosmine; but the resemblance to the typical cosmine of *Megalichthys*, or even to the cosmine of Palæoniscids, is not at all close, and the two structures are probably not homologous. Since in the lepidosteoid scale there are neither pulp-cavities, nor vascular networks giving rise to canaliculi, it seems advisable not to apply to them the name cosmine at all. The tubules, with their inner branching ends, may very well merely represent modified bone-cells, which, instead of being buried in the matrix they produce, get carried outwards further and further from their first position as the scale grows older. They do not all start from the same region. Only the oldest tubules reach the central parts; younger ones start at various points among the later formed laminae. Occasionally the tubules seem to traverse the ganoine in its outer and thinner region; but as a rule they either do not run upwards to the exposed surface or they get cut off by the newly deposited layers of ganoine, each of which of course extends a little further than the last (text-fig. 199).

Text-fig. 199.



(From Lankester's 'Treatise on Zoology,' by permission of Messrs. A. & C. Black.)

Much enlarged view of a piece of the scale of *Lepidosteus osseus* L. *d.*, superficial denticles; *g.*, ganoine layer; *i.*, inner bony layers, or isopodine; *t.*, tubules with branching inner ends; *vc.*, vascular canal.

We have seen what are the three chief kinds of scales commonly called ganoid: to the first it is proposed to give the name cosmoid, while the second and third are varieties of the true ganoid scale. Other and less important varieties exist and will be dealt with later on (p. 765).

#### *Origin of the Cosmoid and Ganoid Scales.*

According to Williamson's theory, which has already been mentioned, the cosmoid scale arose by the fusion of a large number of denticles, and their combination with a bony plate developed below. In fact the theory which we have just found to apply so admirably to the explanation of the plates of the Heterostraci,

was put forward by Williamson to account for the structure of the scales and dermal plates of *Megalichthys* (26). Each pulp-cavity of the cosmine layer is supposed to indicate a single denticle. As representing an intermediate stage in the formation of cosmine, he pointed to the dermal bones of the Cœlacanth *Macropoma*. Here the denticles are clearly seen, either standing up as sharp teeth on the scales, or as more or less blunt protuberances on the cranial bones. The denticles in *Macropoma* retain their histological character and pulp-cavity, although they become fused to the underlying bone, and so deeply sunk in it, that they may be mistaken for a mere superficial ornamentation. Cosmine, says Williamson, is formed by "the confluent aggregation and superficial depression of a number of placoid teeth, surmounting a highly developed scale."

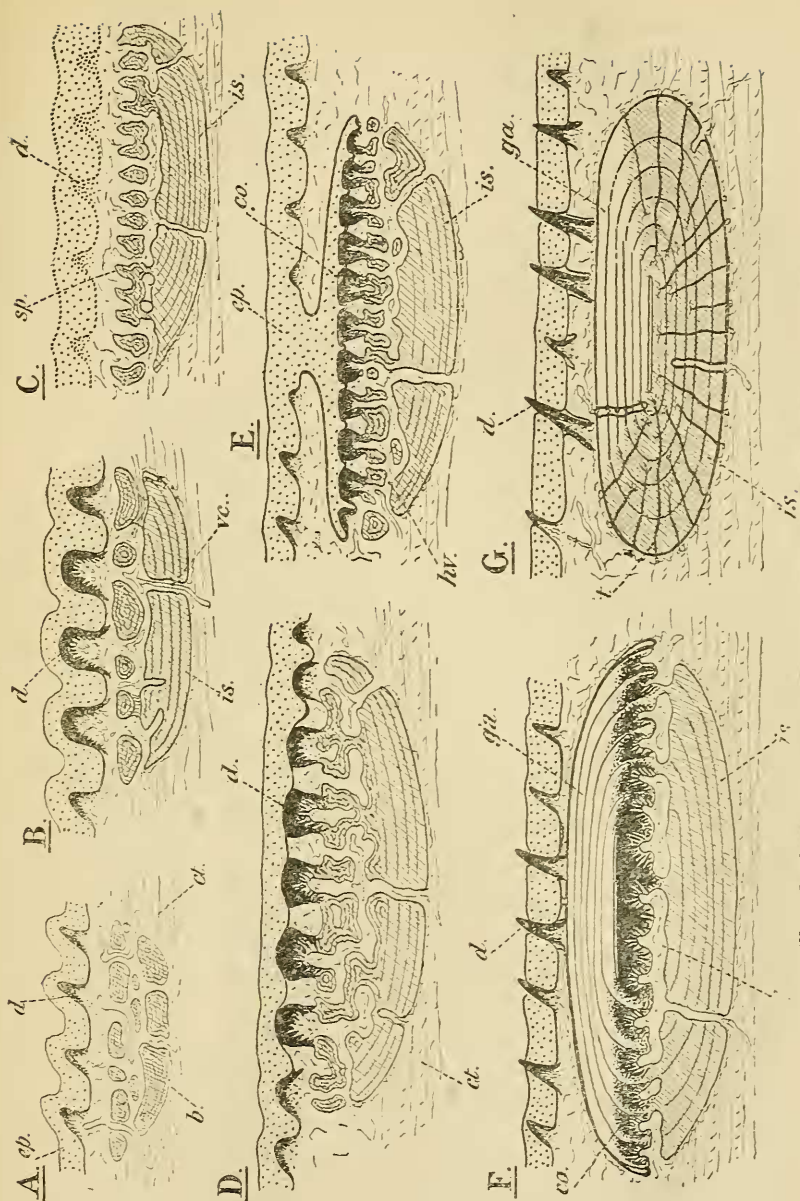
While cosmine grows from within, ganoine is deposited from without. The scale here called Palæoniscoid, Williamson believed to be formed by the overlapping of the bony laminae at the edges, and their spreading out over the outer surface of the cosmine as an enamel-like layer. The ganoid scale, then, would be described as a cosmoid scale the edges of which have been turned over on to the outer surface.

These fascinating theories meet with many difficulties in the way of their adoption; difficulties which are probably not insuperable, but must be disposed of before Williamson's views can be considered as established.

First of all, it is a far cry from the scattered denticles of *Macropoma* to the complex cosmine of the Osteolepids. Most of Williamson's observations on *Macropoma* I can fully confirm. But I have looked in vain for any intermediate forms bridging over the gap between the two types of scale. The dentine-like substance of *Megalichthys* forms a continuous layer, without sign of subdivision externally; and the appearance of a series of crowded denticles seen in a section is chiefly due to the pulp-cavities and conical chambers being cut through alternately. Although so extraordinarily like the shield of *Pteraspis* in section, the two are really very different in structure. In the palæoniscoid scale the cosmine may be said to have lost any trace of the subdivision into separate denticles which it may once have possessed; and in the lepidosteoid scale no true cosmine occurs at all, according to my observations.

Pander, it is true, has given beautiful figures of sections of the dermal bones of *Glyptolepis*, showing how the superficial teeth may become fixed to the bone, and converted into cosmine-like tubercles (15); but I have failed to find anything quite like this in the material at my disposal. On the scales of *Glyptolepis* there appear to be no regularly disposed denticles, though here and there are tubercles which resemble rather the last remnants of disappearing cosmine than the incipient stages in its formation. Rohon, however, agrees with Pander, and supports

Text-fig. 200.



(From Lankester's "Treatise on Zoology," by permission of Messrs. A. & C. Black.)

Diagrams showing the possible origin of the "cosmoid" scale F, the Rhizodont scale C, the "palaeniscoid" scale F, and the "lepidostoid" scale G, from a simple condition A through stage B, or B and D. A, B, D, hypothetical stages showing the fixation of superficial denticles, *d*, on to an underlying bony plate, *b*, pierced by vascular canals, *vc*; *co*, cosmine layer derived from denticles, it is lost in C, and not developed in G. *ct*, connective tissue of cutis; *ga*, outer ganothic laminae; *is*, inner bony laminae; *ep*, epidermis; *sp*, superficial spines and ridges.

the view that the tubercles in "*Dendrodus*" are denticles which have become fused on (19). This is an important point which requires further investigation.

With regard to the ganoid scale new difficulties arise. The cosmine layer in these is supposed to represent the thoroughly fused denticles. Williamson is not explicit on this point, and does not trace in detail the origin of the scale of *Palæoniscus* from that of *Megalichthys*. The denticles, we may suppose, have sunk away from the epidermis, and have become surrounded by concentric layers secreted by the mesodermal pocket in which the scale is now enclosed (text-fig. 200, E & F). But how on such a view can we account for the new formation of cosmine in each successive layer? In the case of the cosmoid scale, the outer layer, we might suggest, remained immediately below the epidermis, new denticles being continually added at the circumference. Such a ring of growth may be compared to a dental groove. These denticles might develop in the ordinary way from "germs" at the edge, and become fixed on during growth (text-fig. 200, D). The thin sheet of transparent substance covering the cosmoid scale would then represent the enamel. But, it may be urged, in the palæoniscoid scale the cosmine would soon become cut off from the epidermis, and it is difficult to see how new "germs" could be produced, and more especially how the newly formed denticles could come to occupy the position of the cosmine in the middle of each lamella at the junction between the ganoiné and the bone. This objection is not fatal, for it must be remembered that the inner secreting surface of the pocket probably represents the original upper surface of the dermis as far as the edge of the scale, and therefore might well retain the power of producing new denticle "germs" at the periphery. In the series of diagrams (text-fig. 200, p. 761) I have endeavoured to illustrate this extension of Williamson's theory in accordance with more recently acquired evidence concerning the development of these various structures.

Of the development of a typical palæoniscoid scale we know nothing; but Nickerson (13) has given us a most excellent account of the development of the scale of *Lepidosteus*, which entirely bears out Williamson's view as to its mode of growth by concentric layers, and I have myself made observations on the development of the scales of *Polypterus* which lead me to the same conclusion.

Let us now examine a third difficulty which suggests itself. It is this: if the denticles are already represented in the cosmine, how comes it that the scales of *Polypterus*, which contain a cosmine layer (p. 770), have denticles set on their outer surface? This question brings us to the consideration of Hertwig's theory of the origin of scales and dermal bones.

Agassiz and Williamson described the denticles which are movably articulated to the surface of the dermal bones of certain Siluroid fish (*Hypostoma*, etc.); and Reissner (17) found

similar small denticles fused to the surface of the scales of *Lepidosteus*. O. Hertwig, in a series of valuable papers on the dermal covering of fish, contributed a number of interesting observations on its structure and development. But, neglecting the work of Williamson, the importance of whose researches he failed to appreciate, Hertwig does not appear to have understood the growth of the ganoid scale, and moreover revived the old and fundamental error of calling the outer layer true enamel. Tracing the origin of all the scales and dermal bones of *Lepidosteus* to the fusion of small plates bearing a denticle, homologous with the placoid scale of the Elasmobranch, Hertwig concluded that originally these fish were provided with a general covering of denticles, that by concrecence their basal plates gave rise to scales, that enamel was deposited where such plates reached the surface, and that subsequently the denticles tended to disappear. Klaatsch, in his important paper on fish-scales (10), supports Hertwig's general theory; but considers that each scale of the higher fish represents a single denticle of which the basal plate has become much enlarged. "Die Ganoidschuppe ist der Placoidschuppe homolog, in so fern sie die alte Einheit fortführt. Sie entspricht in der Hauptmasse der Basalplatte, und zwar den tieferen Theilen derselben. Der Spitzentheil der Placoidschuppe ist rudimentär geworden. Die Ganoinsschicht der Lepidosteusschuppe entspricht den oberflächlichen Theil der Basalplatte. Den Zählchen der Lepidosteusschuppe kommt keine morphologische Bedeutung zu." (p. 155.)

Nickerson also compares the ganoid scale to the placoid denticle on the supposition that the basal plate of the latter has given rise to the scale. The separate development of the dentine cone and of the plate in *Lepidosteus*, he would interpret as due to secondary modification (13).

The denticles on the scales of *Lepidosteus* and *Polypterus* are generally spoken of as degenerate vestigial structures usually absent in the adult, except in certain restricted regions. But there is reason to believe that the denticles are much more abundant and regularly distributed than is commonly supposed. They are to be found in adult specimens of both genera on the scales of the trunk where these have been protected from rough usage. Their absence in many specimens is due to a great extent, if not entirely, to their having been rubbed off. As Nickerson (13) has well shown in *Lepidosteus*, the denticles develop just like those of Elasmobranchs, on the surface of the mesoblastic tissue, and afterwards become fused on to the scale, in the formation of which they take no real part, except in so far as they may occasionally get buried in it. The same is the case in *Polypterus*, as my observations show.

The comparison of the denticle and ganoid scale with the conical apex and basal plate of the placoid denticle seems, therefore, to be fundamentally wrong. As already insisted upon, the basal plate is merely an extension of the denticle cone; there is no

reason to think that it can ever develop separately. Nor is there any evidence that denticles do ever really contribute to form dermal bones. Even in the case of the palatal bones of fish and amphibians, the teeth do not actually combine to build up the supporting bone, but become fused sooner or later to bony substance independently developed at their base.

The history of the palæoniscoid variety of ganoid scale would seem be this (text-fig. 200, p. 761). It first arose as a dermal plate of bone to which became attached a number of denticles, eventually forming an outer layer of cosmine—the cosmoid stage. It then sank deeper into the dermis, which grew over the outer face, and so enclosed it in a mesoblastic pocket secreting complete concentric layers. The outer dermis continued to give rise to denticles, which thus came to be situated on the top of the sunken scale, and subsequently became attached to its surface. Whether the cosmoid scale ever was provided with such denticles is unknown. None have been described in extinct forms; and I have looked for them so far in vain. Possibly the cosmoid scale always remained close under the epidermis, and so there would have been no room for their development. At all events such denticles are only known to occur in *Lepidosteus*, *Polypterus*, and some Siluroids, and the extinct Cœlacanth (which have no true cosmoid or ganoid scales).

This hypothetical history of the cosmoid and palæoniscoid scales is illustrated in the diagrams (text-fig. 200, A to G).

Whether the lepidosteoid variety can be considered as a modification of the palæoniscoid type seems to me extremely doubtful. It is true that the scale of "*Dapidius granulatus*," as described by Williamson, might be taken as intermediate, but my own observations on this species do not confirm his description of cosmine tubules. Indeed this scale appears hardly to differ from the typical lepidosteoid form. Future research on fossil forms may perhaps enable us to determine what has been the history of the lepidosteoid scale—whether it has ever passed through a cosmoid stage.

So far we have merely developed, in a more modern form, Williamson's theory of the origin of the scales of the Teleostomi. It is obvious, however, that another view might be held. The alternative theory which can be put forward is simply this: that the outer layer of the cosmoid scale is merely a special region of the bony plate, which has come to acquire a dentine-like structure, and not a product of superficial denticles. This theory would differ from the first only in its account of the origin of the cosmine; the palæoniscoid scale would still be derived from the cosmoid as explained above. One of the chief difficulties to be met by this view, is that the more primitive and ancient fish (early Dipnoi, and Osteolepidoti (*Crossopterygii*)) have the most perfectly developed cosmine. On the whole Williamson's theory seems the best, though it cannot be considered as fully established

until stages intermediate between the cosmine and the denticle have been discovered.

We have determined what are the three chief kinds of scale; let us now see of what importance they are in classification.

*The Systematic Importance of the Scales in the  
DIPNOI and TELEOSTOMI.*

*The COSMOID type and its derivatives.*—That type of scale which we have called cosmoid occurs only in the extinct Osteolepidoti (Crossopterygii) and in the Dipteridæ. In the thick rhombic scales of the Osteolepidæ it is most perfectly shown. The scale of *Megalichthys* has been fully dealt with above (p. 755). That of *Osteolepis* is quite similar, as may be seen in Pander's excellent figures (15). A section of the edge of the scale of *Osteolepis* is here figured, showing the outer layer of typical cosmine and the absence of stratified ganoine (Pl. XLIII, fig. 5). *Diplopterus* differs scarcely from *Megalichthys* (Williamson).

Now it is extremely interesting to find that the scale of *Dipterus* has exactly the same structure, for it has long been recognised that the Dipteridæ approach the Osteolepidoti (Crossopterygii) more closely than any other group of fish. The importance of this fact is enhanced by the knowledge that the cosmoid type occurs in no other Order. Pander's figures leave no doubt about the resemblance of the scale of *Dipterus* to that of *Osteolepis*. Unfortunately I have not had material favourable for sections; but the fragments I have examined confirm his descriptions. This cosmine layer is of such peculiar, elaborate and complex structure, that we cannot suppose it to have been independently developed in the two cases. There seems no escape from the conclusion that the common ancestor of the Osteolepidæ and Dipnoi had scales of this cosmoid type.

The evidence with regard to the other families of the Osteolepidoti (Crossopterygii) is not so clear. Various forms of scale occur among them; some of which are probably degenerate cosmoid scales, while others perhaps belong to some different though related type.

In the Holoptychiida the scales are usually rounded, and ornamented with tubercles and ridges. Williamson (see his fig. 24, plate 42) figures a section through the scale of *Holoptychius* showing an outer layer which is undoubtedly a stage either in the formation or in the degeneration of the typical cosmine structure. According to Rohon's careful account, the scale of *Holoptychius* (probably another species) is very like that of the Osteolepidæ, excepting for the outer layer. Instead of being built in the uniform and beautifully regular manner of typical cosmine, it is in the form of the irregular tubercles and ridges already mentioned; and these are composed of dentine-like tissue, resembling the cosmine layer of the palæoniscoid scale. There is no alternating system of pulp-cavities and chambers, but merely

a vascular network from which arise branching dentinal tubules. Rohon considers that the tubercles represent denticles fused on to the surface; they appear to me rather to represent stages in the degeneration of cosmine, than in its formation. The same may be said of *Glyptolepis* (p. 760); here the middle vascular layer is to a great extent exposed, forming ridges on the upper face quite similar to those found on the scales of the Rhizodonts.

The scales of the Rhizodontidæ I have been able to examine, such as *Rhizodus*, *Strepsodus*, and *Eusthenopteron*, are rounded, relatively thin, and with a superficial ornamentation of ridges and tubercles (Pl. XLV. fig. 14). The bulk of the scale is made up of the usual parallel bony laminae of isopedine, which merge above into the vascular layer. The ornamentations have no resemblance to cosmine in structure, and are directly continuous with the bony trabeculae of the vascular layer, being formed of the same substance (Pl. XLIV. figs. 6 & 8). Where the tubercles are very large, they appear to be formed to a great extent by the upturning of the isopedine lamellæ at the growing edge of the scale (fig. 7). In some regions of the scale of *Rhizodus* this overturning of the laminae is very pronounced; yet it never results in the deposition of a continuous covering, and only occurs at the edge. Nevertheless, in *Eusthenopteron* and *Rhizodus* the ornamentation seems to have grown, to some extent, by the addition of new bony layers on the outer surface; and we may suppose that, the cosmine having disappeared, the bone-forming cells of the middle layer emerged on the outer face and continued to secrete there. But when once formed, the middle layer itself does not appear to have grown appreciably in thickness, though new laminae were always being added to the lower strata. The ridges are often very numerous and regular, with an elaborate network of canals below opening by many apertures on the surface at the bottom of the valleys. This structure is also seen in *Glyptolepis*; in which, however, here and there the tubercles have the appearance of cosmine (p. 760)\*. *Gyroptychius*, alone among the Rhizodonts, has preserved a thick shiny scale; and here can be seen an outer layer of true cosmine as in *Osteolepis*.

With regard to the Cœlacanthidæ our knowledge is still very incomplete. It has been clearly established by Williamson (26) that some genera such as *Macropoma* have typical denticles, with dentine cone and pulp-cavity, fused on to the outer surface of their scales and dermal bones (p. 760). His account I can fully confirm. The scale consists of an inner layer of isopedine, an intermediate layer with vascular canals, and lastly of the denticles on that hinder region which is not overlapped by neighbouring scales. In *Cœlacanthus* are found the first two layers; but instead of superficial denticles, there are elongated tubercles or shiny ridges which in section appear merely as hollow arches

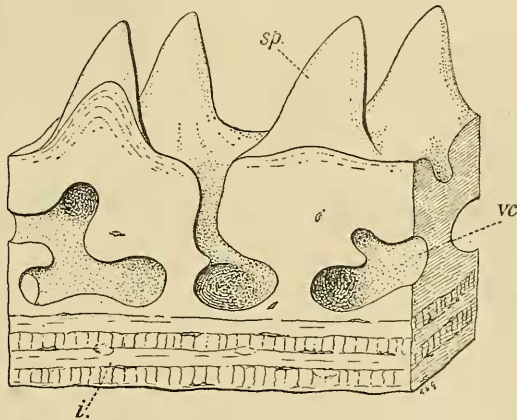
\* We shall await with the greatest interest a description of the scale of *Tarrasius*; doubtless it will throw much light on the problem of the systematic position of this very imperfectly known but important genus.



on the top of the scale (Pl. XLIV. fig. 12). Whether these tubercles represent modified denticles remains to be proved. A careful study of better preserved material, and of other genera, might settle this point.

Turning now to the Dipnoi, we find that *Dipterus* has typical cosmoid scales (p. 765). All the living genera have scales of very uniform structure (Wiedersheim 25, Günther 5, Klaatsch 10); consisting of a basal layer of isopedine lamellæ, little if at all calcified, and an outer calcified layer. The latter closely resembles the outer vascular and ornamental layers of the scale of the Rhizodontidæ. A horizontal network of canals and space runs through the base of the calcified region, and opens by numerous pores between more or less well-defined ridges. A multitude of very small spines projects from the whole surface of the scale. The ridges and partitions separating the vascular spaces grow by the addition

Text-fig. 201.



(From Lankester's 'Treatise on Zoology,' by permission of Messrs. A. & C. Black.)

Enlarged view of a small portion of the scale of *Phaneropteron curtum* Wht.; Upper Devonian, Canada. *i.*, inner bony layer; *sp.*, surface spinelet; *vc.*, vascular space.

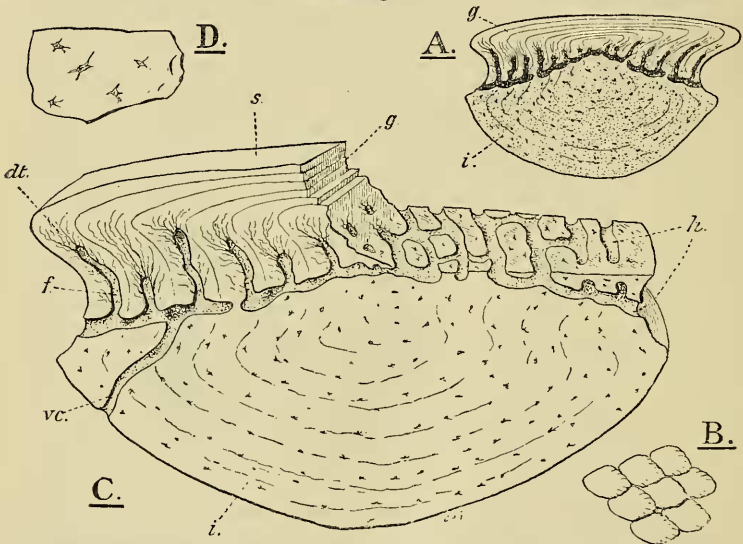
of new laminae of bony substance without cells; and the spines are merely processes of the calcified layer developed in just the same manner. They are obviously analogous to the tubercles on the scale of the Rhizodonts, and like them are found all over the posterior covered as well as generally over the anterior exposed region. These spines have nothing to do with denticles, with which they have been compared by Wiedersheim (25); and differ from them radically both in structure and development. Wiedersheim's theory has already been disposed of by Klaatsch (10). Now it is very interesting to find that this peculiar "Dipnoan" type of scale is already perfectly differentiated in the

Devonian genera, *Phaneropleuron* and *Scaumenacia* (Pl. XLIV. figs. 10 & 11, and text-fig. 201). These fish have thin scales, without cosmine or ganoine, but studded all over with the same characteristic spines. This Dipnoan type of scale would seem to be a degenerate form derived from the cosmoid type of *Dipterus*, after the loss of the cosmine layer. We may expect to find intermediate scales among the other extinct Dipnoi.

THE GANOID SCALES.—Ganoid scales, whether of the palæoniscoid or of the lepidosteoid type, are found only in the Actinopterygii (and Polypterini).

All the Palæoniscidæ and Platysomidæ I have been able to examine, have scales belonging to the Palæoniscoid type, differing

Text-fig. 202.



(From Lankester's 'Treatise on Zoology,' by permission of Messrs. A. & C. Black.)

*Cheirolepis* sp., L. Devonian. A. Transverse section of scale. B. Outer view of scales enlarged. C. Much enlarged view of a piece of a scale cut transversely. D. A fragment of the inner bony layer, magnified. *dt.*, canaliculi of cosmine layer; *f.*, vertical blind canals (pulp-cavities); *g.*, ganoine layer; *h.*, system of horizontal vascular canals; *i.*, inner bony layer, isopedine; *s.*, shiny outer surface; *vc.*, vertical canal.

only in unimportant details (*Palæoniscus elegans*; *Eurynotus crenatus*, text-fig. 198; *Elonichthys*, *Gonatodus*, Pl. XLV. fig. 15). They can be recognised at once in sections by the presence of a network of canals and a layer of cosmine underlying the laminae of ganoine.

The scale of *Cheirolepis*, the structure of which is shown in Pl. XLV. fig. 13 and text-fig. 202, has all these characters well developed in spite of its small size and peculiar shape.

The remainder of the Actinopterygii, except the Teleostei, all appear to have the Lepidosteoid type of scale, with the peculiar tubules described above (p. 758).

*The Protospondyli.*—In the family Semionotidæ, I have examined *Semionotus kappfi*, *Lepidotus mantelli*, and *Dapedius* sp.; in the Pycnodontidæ, *Microdon* sp.; in the Eugnathidæ, *Eugnathus formosus* (Pl. XLVI. fig. 20); in the Pachycormidæ, *Pachycormus heterurus*; and *Ophiopsis* in the Macrosemiidæ. These genera display a remarkably uniform type of lepidosteoid scale. The scales of the Amiidæ (*Amia* and the extinct *Megalurus*) are so thin that little can be made out in sections beyond the fact that they are formed of laminæ and contain bone-cells, except in the topmost layer. However, a section of a cranial dermal bone of *Amia* shows the lepidosteoid tubules developed in the most perfect manner (Pl. XLVI. fig. 18). This observation is of some practical importance, as it may help us to determine the affinity of those fish in which the scales are degenerate or absent, but of which cranial plates can often be obtained\*.

*The Ætheospondyli.*—Both the Aspidorhynchidæ and the Lepidosteidæ show the same characteristic structure; the genera examined being *Lepidosteus* (Pl. XLVI. fig. 16, and text-fig. 199), and *Aspidorhynchus* (fig. 19), already described by Williamson.

It is interesting to find that the scale of *Pholidophorus* also belongs to the Lepidosteoid type.

SUMMARY.—From what has been said in the foregoing pages, it will be gathered that the scales of the Dipnoi and Teleostomi present very few distinct types of structure. That in fact only three distinct types exist: the cosmoid, the palæoniscoid, and the lepidosteoid. Certain other varieties are found, such as the Rhizodont and Dipnoan, which are probably to be derived from the cosmoid. The position of the Cœlacanth scale is at present difficult to determine: it may be a primitive form in which the denticles have not yet fused to a cosmine layer, as Williamson supposed; or it may be simply a degenerate cosmoid scale to the surface of which denticles have become attached.

Further, it appears that the structure of the scales is very uniform within the families, and that closely allied families usually have very similar scales. The cosmoid scale occurs in the extinct Osteolepidoti (Crossopterygii) and Dipnoi; but in no other group of fish. Similarly the ganoid scale occurs in the Teleostomi and never elsewhere. The palæoniscoid type is restricted to the Palæoniscidæ and their immediate allies; while the lepidosteoid type is universal among the Protospondyli, the Ætheospondyli, and the Pholidophoridæ, and not found in any other group as far as is known.

These different kinds of scales, then, are of great systematic value, and the position of a fish in any of the large divisions can

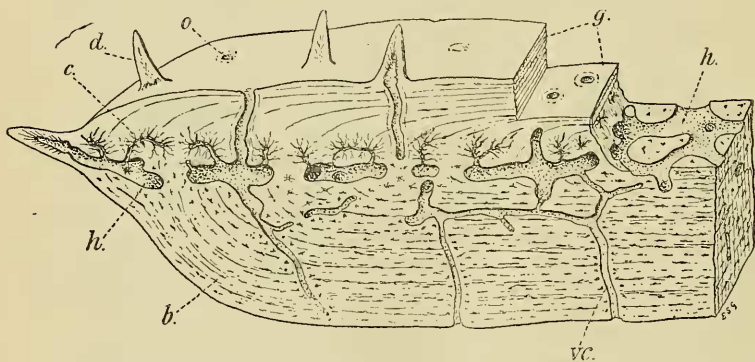
\* Stewart has described similar bone in *Fistularia* (Cat. Coll. Surgeons).

at once be determined by an examination of its scale. Doubtless all the types have been evolved from some common ancestral scale, and numerous intermediate forms will be found, whose position will be difficult to assign; but so far the chief types remain remarkably distinct from each other.\*

*The Scale of POLYPTERUS.*—Let us now apply our test to the scale of *Polypterus*. The Polypterini have always been placed among the so-called Crossopterygii ever since Huxley wrote his famous paper on the classification of Devonian fishes (8). I have elsewhere discussed in greater detail the affinities of *Polypterus* (4); and shall only mention here that, in a paper published some years ago (4*a*), my opinion has already been expressed that its relationship is rather with the Actinopterygii than with extinct "Crossopterygii."

The scale of *Polypterus* has been described by Agassiz (1), Leydig (12), and Hertwig (7). The last author especially

Text-fig. 203.



(From Lankester's 'Treatise on Zoology,' by permission of Messrs. A. & C. Black.)

Portion of a thick transverse section of the scale of *Polypterus bichir* Geoffr., much enlarged. *b.*, inner bony or isopedine layer; *c.*, canaliculi of the cosmine layer; *d.*, superficial denticle; *g.*, ganoine layer; *h.*, system of horizontal vascular canals; *o.*, opening of vertical canal on outer surface; *vc.*, vertical canal.

has contributed much information concerning the histological structure of the scale itself, and the denticles which become attached to its surface (p. 763).

A glance at text-fig. 203 will show at once that the scale of

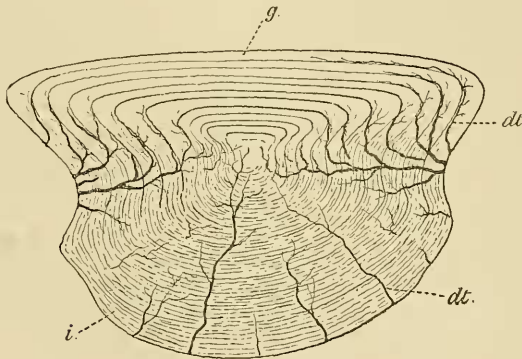
\* Since this was written I have found a paper, which unfortunately escaped my notice, by Dr. H. Scupin ("Zur Histologie der Ganoidschuppen," Arch. f. Naturg. vol. lxii. 1896), in which the microscopic structure of fish-scales is dealt with.

*Polypterus* is of the ganoid type; and, moreover, that it belongs to the paleoniscoid variety. For in it can be seen not only the concentric layers of bone below and ganoine above, but also the intermediate horizontal network of vascular canals, and the cosmine-like layer supplied by narrow canals from which spring numberless dentinal tubules. No scale of this kind is known outside the Actinopterygii. The evidence is quite clear and definite: the scale is of the true ganoid type, and approaches that of the Palæoniscoid more closely than any other. Not for a moment is it asserted that *Polypterus* is a living Palæoniscoid; but it is probably in the neighbourhood of this family that it will eventually find its place in the system of classification.

*The ACANTHODII.*—The scales of the Acanthodii are of very uniform structure, usually in the form of a mosaic of very small closely fitting, thick, rhomboidal plates, set in oblique rows like the ganoid scales of a Teleostome.

They have always been compared to those of the Elasmobranchs, and are generally spoken of as modified denticles, in which the pulp-cavity has become reduced. Rohon (18), Reis (16), and

Text-fig. 204.



(From Lankester's 'Treatise on Zoology,' by permission of Messrs. A. & C. Black.)

Transverse section of the scale of *Acanthodes* sp.; L. Carboniferous, Edinburgh.  
*dt.*, branching canaliculi; *g.*, outer shiny layer; *i.*, inner more opaque layer.

Fritsch (2) have given descriptions of the scales of various Acanthodians.

The chief features of the structure of the scale of *Acanthodes* are shown in the semi-diagrammatic text-figure 204, and in fig. 21 (Pl. XLVI.), which represents a section taken parallel to the upper surface. It is at once clear that it differs radically from the placoid denticle in its mode of growth, which is by the addition of complete

concentric layers, just as in a ganoid scale. Neither in this nor in any other species that I have examined, from Devonian, Carboniferous or Permian rocks, can I find the slightest trace of the small pulp-cavity the presence of which is asserted by Rohon, but denied by Reis. Nor does the structure of the scale seem to me to afford any evidence whatever of such a cavity having been present. Reis and others have already described dentinal tubules passing inwards from the periphery. These run in towards the centre, at right angles to the lines of growth, from all the circumference except the top; and are specially numerous about half way up the scale, where a slight constriction separates the upper from the lower region. Only a few tubules reach the middle, most of them stop short at varying distances from the edge.

The outer or upper region of the scale appears more dense than the lower; it is not pierced by tubules from above, but some of them penetrate far into the superficial laminae from the sides. No bone-cells are present.

The Acanthodian scale, with its concentric laminae and upper ganoine-like layers, bears a striking resemblance to the ganoid scale of the Teleostome. Moreover, the distribution of the branching dentinal tubules is quite like that of the similar tubules of the lepidosteoid type of scale, excepting for their more extensive spreading on to the upper surface. There are no vascular canals, a fact which may be correlated with the small size of the scale.

Whatever may be the origin of the Acanthodian scale, there can be no doubt that it is built on a quite different plan from that of the placoid, and that it approaches most nearly to the lepidosteoid type. Fritsch (2) figures scales of *Traquairia* and *Protacanthodes* with a tooth-like process on the hinder edge; unfortunately he gives no information as to the histological structure of these scales, so that it cannot be determined whether the process represents a pointed extremity or a denticle fused on.

At present we know too little concerning the scales of the Acanthodii, to draw any conclusion from their structure as to the phylogeny of the group. But these scales should no longer be vaguely called modified denticles, and used as evidence of affinity with the Elasmobranchs.

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